Journal of Applied Ecology

British Ecological Society

Journal of Applied Ecology 2011, **48**, 143–147 doi: 10.1111/j.1365-2664.2010.01899.x

FORUM

Connectivity, dispersal behaviour and conservation under climate change: a response to Hodgson *et al.*

Veronica A. J. Doerr[1,2]*, Tom Barrett[3] and Erik D. Doerr[1,2]

[1]*CSIRO Ecosystem Sciences, GPO Box 284, Canberra ACT 2601, Australia;* [2]*Research School of Biology, Australian National University, Canberra ACT 0200, Australia; and* [3]*New South Wales Department of Environment, Climate Change & Water, PO Box 494, Armidale NSW 2350, Australia*

Summary

1. Hodgson *et al.* [*Journal of Applied Ecology* **46** (2009) 964] argue that connectivity is complex and uncertain, that it can be improved incidentally by increasing habitat extent, and that connectivity conservation is unlikely to be effective under climate change.

2. We believe that they have overlooked recent research on dispersal behaviour and structural connectivity, which has improved our understanding of functional connectivity and revealed that it will not necessarily increase with habitat extent.

3. New modelling techniques including least-cost path models incorporate this more detailed understanding of connectivity into conservation planning, facilitating the true aim of connectivity conservation – to ensure appropriate interactions between habitat extent, quality and connectivity.

4. *Synthesis and applications*. Advances in behavioural research and modelling techniques allow us to manage structural connectivity with as much certainty as we manage extent and quality of habitat. Successful landscape conservation to address both current threats and future climate change must manage these three elements in concert.

Key-words: aggregation, behavioural ecology, connectivity conservation, corridor, fragmentation, gap-crossing, metapopulation, population viability, range shift, stepping stone

Introduction

For most of the world's ecosystems, human-induced habitat loss, degradation and fragmentation are primary causes of declines in biodiversity (Fahrig 2003; Lindenmayer & Fischer 2006). Furthermore, climate change is predicted to interact with and intensify the effects of these problems. 'Connectivity conservation' has emerged as an overarching solution with considerable political and popular support (Crooks & Sanjayan 2006). However, Hodgson *et al.* (2009) highlight the dangers of investing in connectivity *per se*, and argue that other strategies may provide better protection for species in a changing climate.

We wholeheartedly agree with Hodgson *et al.* that connectivity should not be the sole focus of conservation actions, and that conservation investments should be based on analysis of their likely benefits. Yet Hodgson *et al.* suggest that connectivity conservation is never likely to be a robust strategy, and here we disagree. Specifically, Hodgson *et al.* argue that there is too much uncertainty surrounding connectivity, that connectivity is primarily a result of habitat aggregation, and it can coincidentally be improved by increasing habitat extent. They also suggest that connectivity conservation sacrifices long-term conservation success under a changing climate in favour of short-term gains. In this response, we suggest that Hodgson *et al.* have overlooked recent advances in our understanding of connectivity, particularly arising from research on dispersal behaviour. These advances provide a clearer distinction between structural and functional connectivity and greater certainty regarding the effects of structural connectivity. They also bring a new awareness that increases in habitat extent alone will not necessarily increase functional connectivity. In addition, we believe that Hodgson *et al.* have misinterpreted connectivity conservation, which carries a specific meaning that involves more than just conserving structural connectivity, and can provide long-term solutions to many of the threats associated with climate change including those highlighted by Hodgson *et al.* Finally, we suggest that the differences in our perspectives may partly result from differences in the scales at which empirical research and conservation planning are conducted. Fortunately, new modelling techniques are allowing us

*Correspondence author. E-mail: veronica.doerr@csiro.au

to move beyond simple measures of aggregation to incorporate a more detailed behavioural understanding of connectivity into conservation planning, despite differences in scale.

Dispersal behaviour and structural connectivity

The intent of connectivity is to facilitate dispersal of individuals. Thus, an empirical understanding of connectivity depends on understanding animal behaviour, particularly movement and dispersal behaviour, to reveal what parts of landscapes individuals are willing to move through and why (Lima & Zollner 1996; Chetkiewicz, Clair & Boyce 2006). The value of behavioural research for conservation has been debated (Blumstein & Fernandez-Juricic 2004; Caro 2007), and thus it is unsurprising if conservation biologists are not familiar with the movement behaviour literature, very little of which existed during early discussions about connectivity. Yet movement behaviour is a rapidly growing field (Nathan 2008), with extensive empirical analyses and emerging theories that can provide a strong foundation for modelling and conserving connectivity.

When connectivity began to be viewed from a behaviour-based perspective, it became a characteristic of the matrix between subpopulations (Taylor, Fahrig & With 2006), rather than a characteristic of patches or landscapes. Movement could be dependent not just on distances between subpopulations (i.e. aggregation) but on the physical characteristics of the matrix itself, particularly the presence of habitat elements too small for settlement but which might nonetheless facilitate movement. As a result, a much clearer distinction emerged between structural and functional connectivity. 'Structural connectivity' refers to physical characteristics of the landscape between patches of occupied habitat. 'Functional connectivity' refers to the degree to which movement of individuals and/or their genetic material actually occurs, and is influenced by both movement potential due to structural connectivity and by local subpopulation dynamics (Hilty, Lidicker & Merenlender 2006).

Empirical research on movement behaviour has concentrated on revealing what types of structural connectivity provide the potential for dispersal movements and thus contribute to functional connectivity. A number of studies have shown that various species use corridors to move through fragmented landscapes (Haddad *et al.* 2003; Haddad & Tewksbury 2005), and some have demonstrated the use of simpler landscape elements such as scattered trees (Fischer & Lindenmayer 2002; Doerr, Doerr & Davies 2010). Research on gap-crossing behaviour has been particularly critical, identifying gap distances either within corridors or among scattered trees that may prevent movements, thus revealing details of structural connectivity that contribute to movement potential (St. Clair *et al.* 1998; Grubb & Doherty 1999; Robertson & Radford 2009). In addition, research on overall movement strategies such as foray search is illustrating that distances between subpopulations (i.e. aggregation) may have a threshold effect rather than a linear effect on movement potential. When individuals use a foray-based search strategy, they may have a maximum search distance beyond which they will not travel, regardless of how much structural connectivity is present in the landscape (Conradt, Roper & Thomas 2001; Doerr & Doerr 2005; Doerr, Doerr & Davies 2010).

The species-specific nature of behavioural research may be viewed as an impediment to its usefulness for ecosystem conservation, but patterns are emerging which suggest that responses to structural connectivity may not be as species-specific as was once thought (Haddad *et al.* 2003; Doerr, Doerr & Davies 2010; Gilbert-Norton *et al.* 2010). Instead, movement behaviour may be shaped by the structure of environments experienced over evolutionary time, and species in any given ecological community with broadly similar life-histories may have evolved similar movement behaviours as responses to their shared environments (Fahrig 2007). For example, Doerr, Doerr & Davies (in press) found that use of scattered trees, foray distances, and gap distances crossed were similar among five Australian woodland birds despite substantial differences in their ecology. Belisle (2005) proposed that travel costs may provide one mechanism through which landscapes can exert similar evolutionary pressures across species. Thus, theories from behavioural ecology such as the marginal value theorem could provide the basis for general theories of connectivity, allowing us to predict the effects of different types of structural connectivity for large suites of species at once (Belisle 2005).

Conservation certainty

All of these advances are making structural connectivity a much more measurable and manageable concept than Hodgson *et al.* suggest. Functional connectivity remains complex because it integrates movement potential with the dynamics of subpopulations (which is why Hodgson *et al.* deem it too intractable for conservation planning). Yet structural connectivity contributes significantly to functional connectivity by determining movement potential. The resulting effects on population persistence are also increasingly predictable thanks to controlled research in experimental landscapes which is demonstrating that connected patches experience fewer local extinctions than isolated patches (Damschen *et al.* 2006; Brudvig *et al.* 2009). Thus, structural connectivity can be directly quantified in the landscape, has predictable effects on movement potential, and is known to contribute to population persistence, making it a worthwhile focus for management.

Unfortunately, Hodgson *et al.* omit structural connectivity from their schematic of the place of connectivity in conservation (Hodgson *et al.*, Fig. 2). We have revised their diagram to distinguish between structural and functional connectivity and depict the relationships between them, as well as relationships with the area and quality of habitat suitable for settlement (Fig. 1). Structural connectivity is independent of habitat area and quality and is what defines habitat for dispersal, just as area and quality are what define habitat for settlement. Structural connectivity, habitat area and quality interact to determine functional connectivity, but they also interact to determine subpopulation dynamics and thus the effective

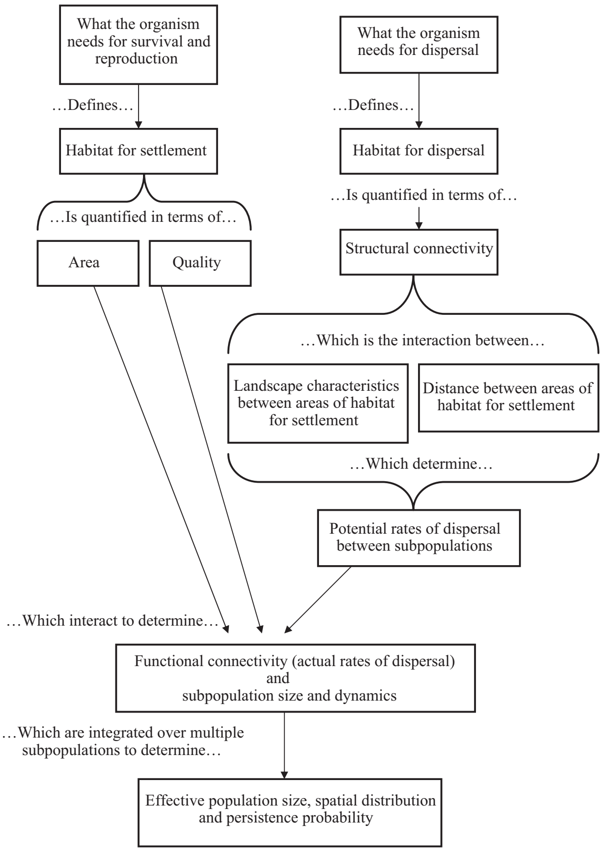

Fig. 1. A schematic illustrating the role of both structural and functional connectivity in spatial ecology and conservation (revised from Fig. 2 in Hodgson *et al.* (2009)). Functional connectivity results from interactions between the amount and quality of habitat suitable for settlement as well as the influence of the rest of the landscape (i.e. structural connectivity) on the potential for dispersal. Structural connectivity is therefore a vital component of functional connectivity that is tractable to model and manage.

population size of the population as a whole. None has a direct influence on populations completely independent of the others – all provide the same degree of conservation certainty because their benefits depend on the interactions between them.

Hodgson *et al.* also argue we can be relatively certain about the positive effects of increasing habitat extent and habitat quality – often assumed to be accomplished through increasing the size and/or number of protected areas. Yet in highly disturbed ecosystems, there may be little habitat left outside of already existing protected areas. Thus, increasing habitat extent and improving habitat quality involves restoring habitat in areas where it has been lost to other land uses. Unfortunately, there are substantial limitations and uncertainties in our ability to restore ecosystems. For example, nitrogen enrichment via fertilisation reduces plant diversity as well as the stability of ecosystems worldwide (McIntyre 2008; Bai *et al.* 2010). These effects can last long after fertilisation has ceased, inhibiting full recovery of the ecosystem despite restoration attempts (Munro *et al.* 2009). It is also reasonable to argue that habitat quality will often be more species-specific than structural connectivity, as habitat for settlement must provide for many more of a species' needs than habitat for dispersal (Haddad & Tewksbury 2005; Doerr, Doerr & Davies 2010). Restoring habitat for settlement, either for a single species or particularly for an entire community, may thus be more complex and uncertain than restoring habitat for dispersal (i.e. increasing structural connectivity).

Finally, Hodgson *et al.* argue that increasing habitat extent will coincidentally improve connectivity by increasing aggregation and thus reducing distances between patches. However, behavioural research suggests that reducing inter-patch distances without providing structural connectivity will only be beneficial once patches become close enough to allow gap-crossing between them. That distance may be as little as 60–100 m (unlikely to be achieved by most efforts to increase habitat extent), as many species are unwilling to cross gaps any larger (Desrochers & Hannon 1997; Robertson & Radford 2009; Doerr, Doerr & Davies 2010). Individuals can traverse much greater distances between habitat patches if structural connectivity is present, but the existence of foray-based search means that increases in aggregation may only be beneficial if distances between patches can be reduced below a critical foray distance threshold, which may only be 1–2 km (Doerr, Doerr & Davies 2010, in press). Thus, the benefits of reducing aggregation *per se* (as opposed to managing it in concert with structural connectivity) are risky because they are not commensurate with effort.

'Connectivity conservation' is more than just conserving connectivity

Hodgson *et al.* interpret connectivity conservation as the effort to increase structural connectivity with the primary purpose of enabling species' range shifts due to climate change. However, as highlighted above, structural connectivity interacts with other aspects of the landscape and thus is not necessarily the sole or most important aspect to improve in every landscape. Connectivity conservation acknowledges this, and has a very specific meaning in the literature (IUCN WCPA 2006; Worboys 2010), much like 'systematic conservation planning' has a specific meaning and doesn't merely refer to taking a systematic approach to planning conservation actions (Margules & Pressey 2000). As a result, connectivity conservation is broader than Hodgson *et al.*'s interpretation.

Connectivity conservation can be defined as coordinated efforts to achieve metapopulation viability across a range of spatial scales, which involves evaluating and improving *the interactions between* habitat area, habitat quality and structural connectivity (Crooks & Sanjayan 2006; Worboys 2010). There is no overarching rule about which action is always more effective – this depends on the existing conditions in a given landscape. Connectivity conservation thus aims to develop flexible solutions, tailored to the different needs of different landscapes. This may involve protecting large continuous areas of existing habitat, but may also involve protecting or increasing connections between multiple small discontinuous areas of habitat where that is all that remains. The preference of Hodgson *et al.* to focus on habitat area and habitat quality can thus be

encompassed by connectivity conservation wherever these actions are deemed to provide the greatest benefits.

Finally, the ultimate purpose of connectivity conservation is not simply to facilitate range shifts, but to increase the resilience of populations to the variety of threats caused by or intensified by climate change. Under connectivity conservation, structural connectivity is desired where it links multiple subpopulations via dispersal, allowing subpopulations to function collectively as one larger, more resilient population. These principles can be applied at any scale, not just scales that might be relevant for possible range shifts under climate change (Opdam & Wascher 2004). Thus, connectivity conservation can be used to reduce pressures other than climate change, can be applied to increase viability of populations in centres of endemism, and can concentrate on areas of high environmental heterogeneity – all of which are principles that Hodgson *et al.* suggest will underlie robust conservation strategies under climate change.

Moving beyond aggregation in large-scale conservation planning models

Conservation modellers may still be unsure how to incorporate advances in our understanding of connectivity and connectivity conservation due to the different scales at which behavioural research and conservation planning are usually conducted. Conservation planning often occurs at very large scales – regions to global scales. Yet a behavioural understanding of connectivity is shaped at scales relevant to movement of individuals – local to landscape scales. The difficulty is that incorporating small-scale detail in large-scale models is often deemed computationally intractable. Fortunately, there are promising new advances that can model connectivity over large spatial scales in ways that align more closely with a behaviour-based view of connectivity.

First, we have already noted that the types of structural connectivity that facilitate dispersal movements are not necessarily species-specific. Thus, models may only need to incorporate general principles (such as threshold distances between habitat patches) rather than behavioural detail specific to many different species. Another way in which conservation planning models can incorporate a tractable amount of behavioural detail is through the use of least-cost path modelling and state-space modelling. These new types of models simultaneously explore behavioural and landscape parameters to identify which landscape details most need to be incorporated into large-scale models (Chetkiewicz, Clair & Boyce 2006; Kadoya 2009), which can then be kept relatively simple by modelling only the few most relevant small-scale parameters. Remaining computational challenges can often be overcome by decreasing the sizes of grid cells only to a relevant scale. Further behavioural detail can then be incorporated by modelling resistance of grid cells that have different compositions (McRae & Beier 2007).

One example of the success of these new approaches comes from our own work, in which data on gap-crossing distances (Doerr, Doerr & Davies 2010) were used to define the maximum distance individuals will move through non-habitat, and data on foray-based search behaviour and foray distances (Doerr & Doerr 2005; Doerr, Doerr & Davies 2010) were used to define the maximum distance individuals will move through structural connectivity, modelled as suboptimal habitat. Using modern satellite imagery, suboptimal habitat could be mapped at a fine scale of resolution to detect very small elements of structural connectivity known to support dispersal movements, such as single trees. Fine-scale habitat mapping and simplified behavioural rules were then modelled together using the least-cost path approach (Drielsma, Manion & Ferrier 2007), with habitat quality as a surrogate for movement cost. This modelling approach simultaneously evaluates habitat area, quality and structural connectivity, identifying where these elements currently exist in concert in the landscape versus where they are unable to interact due to deficiencies in one or more elements (Barrett *et al.* 2010). This gives conservation planners the ability to make practical recommendations that maximise the likelihood that actions at a local scale will contribute to population viability and resilience at large scales (Barrett *et al.* 2010). These models are currently being used to guide conservation planning decisions in several regions of New South Wales, Australia.

Reasons to be cheerful – indeed!

As Hodgson *et al.* suggest, it is easy to be overwhelmed by the challenges of conservation under climate change. It is worthwhile returning to basic principles, focusing on actions that will be cost-effective and that will address current threats as well as those anticipated due to climate change. Fortunately, connectivity conservation provides such an approach by focusing on habitat area, quality, and structural connectivity as independent attributes that must all work together to support viable, resilient populations. Thanks to a growing body of behavioural research, we can reliably identify situations in which fostering structural connectivity in the matrix is likely to yield positive benefits for populations. We can also use behavioural information to model connectivity alongside habitat extent and quality and thus tailor management to specific landscapes. Ultimately, these new techniques ensure that large-scale conservation planning can take advantage of up-to-date connectivity knowledge to truly provide evidence-based conservation guidance.

Acknowledgements

Thanks to members of the Great Eastern Ranges Initiative, David Westcott, Paul Sunnucks, Sasha Pavlova, and Colleen Cassady St. Clair for discussions that shaped these ideas. The manuscript was greatly improved by the comments of Richard Fuller, Sue McIntyre, Dan Lunney, Vicki Logan, and five anonymous reviewers.

References

Bai, Y.F., Wu, J.G., Clark, C.M., Naeem, S., Pan, Q.M., Huang, J.H., Zhang, L.X. & Han, X.G. (2010) Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: evidence from inner Mongolia Grasslands. *Global Change Biology*, **16**, 358–372.

Barrett, T., Drielsma, M., Love, J., Howling, G. & Anderson, G. (2010) *Modelling of Fauna Habitat and Connectivity Values to Support Conservation Planning Decisions in the Hunter Region of NSW as Part of the Great Eastern*

Ranges Initiative. New South Wales Department of Environment, Climate Change and Water, New South Wales.

Belisle, M. (2005) Measuring landscape connectivity: the challenge of behavioral landscape ecology. *Ecology*, **86**, 1988–1995.

Blumstein, D.T. & Fernandez-Juricic, E. (2004) The emergence of conservation behavior. *Conservation Biology*, **18**, 1175–1177.

Brudvig, L.A., Damschen, E.I., Tewksbury, J.J., Haddad, N.M. & Levey, D.J. (2009) Landscape connectivity promotes plant biodiversity spillover into non-target habitats. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 9328–9332.

Caro, T. (2007) Behavior and conservation: a bridge too far? *Trends in Ecology & Evolution*, **22**, 394–400.

Chetkiewicz, C.L.B., Clair, C.C.S. & Boyce, M.S. (2006) Corridors for conservation: integrating pattern and process. *Annual Review of Ecology Evolution and Systematics*, **37**, 317–342.

Conradt, L., Roper, T.J. & Thomas, C.D. (2001) Dispersal behaviour of individuals in metapopulations of two British butterflies. *Oikos*, **95**, 416–424.

Crooks, K.R. & Sanjayan, M., ed. (2006) *Connectivity Conservation*. Cambridge University Press, Cambridge.

Damschen, E.I., Haddad, N.M., Orrock, J.L., Tewksbury, J.J. & Levey, D.J. (2006) Corridors increase plant species richness at large scales. *Science*, **313**, 1284–1286.

Desrochers, A. & Hannon, S.J. (1997) Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology*, **11**, 1204–1210.

Doerr, E.D. & Doerr, V.A.J. (2005) Dispersal range analysis: quantifying individual variation in dispersal behaviour. *Oecologia*, **142**, 1–10.

Doerr, V.A.J., Doerr, E.D. & Davies, M.J. (2010) *Systematic Review #44: Does Structural Connectivity Facilitate Dispersal of Native Species in Australia's Fragmented Terrestrial Landscapes?* Collaboration for Environmental Evidence, Bangor.

Doerr, V.A.J., Doerr, E.D. & Davies, M.J. (in press) Dispersal behaviour of Brown Treecreepers predicts functional connectivity for several other woodland birds. *Emu*.

Drielsma, M., Manion, G. & Ferrier, S. (2007) The spatial links tool: automated mapping of habitat linkages in variegated landscapes. *Ecological Modelling*, **200**, 403–411.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics*, **34**, 487–515.

Fahrig, L. (2007) Non-optimal animal movement in human-altered landscapes. *Functional Ecology*, **21**, 1003–1015.

Fischer, J. & Lindenmayer, D.B. (2002) The conservation value of paddock trees for birds in a variegated landscape in southern New South Wales. 2. Paddock trees as stepping stones. *Biodiversity and Conservation*, **11**, 833–849.

Gilbert-Norton, L., Wilson, R., Stevens, J.R. & Beard, K.H. (2010) A meta-analytic review of corridor effectiveness. *Conservation Biology*, **24**, 660–668.

Grubb, T.C. & Doherty, P.F. (1999) On home-range gap-crossing. *The Auk*, **116**, 618–628.

Haddad, N.M. & Tewksbury, J.J. (2005) Low-quality habitat corridors as movement conduits for two butterfly species. *Ecological Applications*, **15**, 250–257.

Haddad, N.M., Bowne, D.R., Cunningham, A., Danielson, B.J., Levey, D.J., Sargent, S. & Spira, T. (2003) Corridor use by diverse taxa. *Ecology*, **84**, 609–615.

Hilty, J.A., Lidicker, W.Z. & Merenlender, A.M. (2006) *Corridor Ecology: The Science and Practice of Linking Landscapes for Biodiversity Conservation*. Island Press, Washington, D.C.

Hodgson, J.A., Thomas, C.D., Wintle, B.A. & Moilanen, A. (2009) Climate change, connectivity and conservation decision making: back to basics. *Journal of Applied Ecology*, **46**, 964–969.

IUCN WCPA (2006) Papallacta Declaration. *Mountain Forum Bulletin*, **7**, 46.

Kadoya, T. (2009) Assessing functional connectivity using empirical data. *Population Ecology*, **51**, 5–15.

Lima, S.L. & Zollner, P.A. (1996) Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution*, **11**, 131–135.

Lindenmayer, D.B. & Fischer, J. (2006) *Habitat Fragmentation and Landscape Change: An Ecological and Conservation Synthesis*. Island Press, Washington, D.C..

Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.

McIntyre, S. (2008) The role of plant leaf attributes in linking land use to ecosystem function in temperate grassy vegetation. *Agriculture Ecosystems & Environment*, **128**, 251–258.

McRae, B.H. & Beier, P. (2007) Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 19885–19890.

Munro, N.T., Fischer, J., Wood, J. & Lindenmayer, D.B. (2009) Revegetation in agricultural areas: the development of structural complexity and floristic diversity. *Ecological Applications*, **19**, 1197–1210.

Nathan, R. (2008) An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 19050–19051.

Opdam, P. & Wascher, D. (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, **117**, 285–297.

Robertson, O.J. & Radford, J.Q. (2009) Gap-crossing decisions of forest birds in a fragmented landscape. *Austral Ecology*, **34**, 435–446.

St. Clair, C.C., Belisle, M., Desrochers, A. & Hannon, S. (1998) Winter responses of forest birds to habitat corridors and gaps. *Conservation Ecology [online]*, **2**, 13.

Taylor, P.D., Fahrig, L. & With, K.A. (2006) Landscape connectivity: a return to the basics. *Connectivity Conservation* (eds K.R. Crooks & M. Sanjayan), pp. 29–43. Cambridge University Press, Cambridge.

Worboys, G.L. (2010) The connectivity conservation imperative. *Connectivity Conservation Management – A Global Guide* (eds G.L. Worboys, W.L. Francis & M. Lockwood), pp. 3–21. Earthscan, London.

Received 16 June 2010; accepted 20 October 2010
Handling Editor: Morten Frederiksen